THE PLANTAGINACEAE IN THE SOUTHEASTERN UNITED STATES[1]

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PLANTAGINACEAE A. L. de Jussieu, Gen. Pl. 89. 1789, "Plantagines," nom. cons.

(PLANTAIN FAMILY)

A small family of terrestrial [to aquatic], mostly acaulescent herbs [or occasionally woody subshrubs] with simple, usually alternate, exstipulate leaves. Flowers mostly perfect, small, inconspicuous, usually numerous in cylindrical [to capitate] axillary spikes, mostly proterogynous and wind pollinated. Perianth for the most part actinomorphic and membranaceous-scarious. Sepals 4 [rarely 3], imbricate, the margins glabrous to [rarely long-]ciliate. Corolla salverform [or rarely the lobes indistinct] with 4 (sometimes 2) [rarely 1] stamens alternate with the petals, anthers versatile, filaments long and adnate to the tube. Gynoecium of 2 completely connate carpels, the style filiform, the ovary

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superior, 2- [rarely 1-]locular, with 1 to many anatropous to hemianatropous ovules per locule and axile [or basal or subbasal] placentation. Fruit a circumscissile [or rarely indehiscent] capsule [or stony achene]. Seed with a longitudinally [rarely transversely] oriented embryo in fleshy endosperm, the seed coat more or less mucilaginous when wet. (Including Littorellaceae S. F. Gray; Psylliaceae Horaninow, nomen superfluum.) TYPE GENUS: *Plantago* L.

Three genera and 220–275 species; represented in the southeastern United States by 12 (or perhaps 13) species of *Plantago,* a widely distributed and polytypic genus. *Plantago* differs from *Bougueria* Dcne. and *Littorella* Berg. in its axile (vs. basal or subbasal) placentation, its two-locular (vs. one-locular) ovary, and its two- to many-seeded (rarely one-seeded), circumscissile capsule (vs. stony achene). Barnéoud divided the family into two tribes, primarily on the basis of these differences in fruit.

The three species of *Littorella* (*L. uniflora* (L.) Ascherson, $2n = 24$, of western and central Europe; *L. americana* Fern., $2n = 24$, of northeastern North America; and *L. australis* Griseb. ex Bentham & Hooker, of Chile and Argentina) occur on the shores of lakes and ponds and the margins of quiet streams. They are monoecious herbs with spicate inflorescences in which two carpellate flowers are nearly at ground level and are separated from a single, subterminal flower. (In *L. australis* the carpellate and staminate flowers may be more numerous and less separated.) The carpellate flowers develop one essentially sessile ovule, and at maturity the embryo is parallel to the long axis of the seed. In the single, slightly woody species of *Bougueria* (*B. nubicola* Dcne., $2n = 12$), a poorly collected plant of the high Andes in Peru, Bolivia, and Argentina, the inflorescence is a congested capitate spike in which perfect flowers are lower and more numerous than carpellate ones (although opinion varies on this point). The solitary ovules of both types of flowers are stalked, and at maturity the embryo is perpendicular to the long axis of the seed.

The various proposed affinities of the Plantaginaceae have been much disputed, although several authors have suggested an alliance with the Plumbaginaceae and/or Primulaceae, and in more recent years a relationship with the Scrophulariaceae has attained a certain level of acceptance.

Endlicher united the Plantaginaceae and the Plumbaginaceae in his "Plumbagines" despite the fact that members of the Plumbaginaceae have five-merous flowers, stamens opposite the petals, and seeds with a mealy endosperm. Decaisne compared the Plantaginaceae with the Primulaceae, some members of which have circumscissile capsules, and Bentham and Hooker placed them near the end of their "Gamopetalae," calling it an anomalous family reminiscent of the endospermous Acanthaceae in seed structure and insertion. The family was positioned between the Phrymaceae and the Rubiaceae in *Die natürlichen Pflanzenfamilien* (see Harms & Reiche), and Bessey included it with the Primulaceae and the Plumbaginaceae in his Primulales. Hutchinson (1959) put the family in a monotypic order immediately after the Plumbaginaceae (Primulales) and before the Crassulaceae (Saxifragales). Melchior positioned an identically circumscribed Plantaginales between the Solanales and the Dipsacales (and the family between the Phrymaceae and Caprifoliaceae).

Airy Shaw (in Willis) proposed that the Plantaginaceae are allied with the Scrophulariaceae, stating that the "flower is usually regarded as derived from a five-merous type in the same way [i.e., by suppression of one calyx lobe and complete fusion of two corolla lobes] as that of *Veronica* (Scrophulariaceae), and there are good grounds (including entomological, *viz.* the food-plants of certain Lepidoptera and Coleoptera) for believing that the Plantaginaceae are in fact allied to Scrophulariaceae." Most subsequent authors have conceded such a relationship. Thorne (1976) placed the family in his Bignoniales (with six other families) between the Scrophulariaceae and the Lentibulariaceae. Dahlgren included it in the Scrophulariales (composed of Thorne's Bignoniales and ten other families). Takhtajan put it in the suborder Scrophulariineae between the Gesneriaceae and the Lentibulariaceae and stated that the Plantaginaceae are "near to and derived from Scrophulariaceae." Cronquist (1981) more or less agreed with such an ancestry, but he nevertheless maintained the Plantaginales as a distinct order. (Although Cronquist earlier [1968] had noted that without anemophily and the persistent, scarious corolla, the Plantaginaceae could be positioned in the Polemoniales, he also pointed out that the occurrence in the family of both micropylar and chalazal haustoria was in agreement with a relationship to the Scrophulariaceae.)

Numerous studies have indicated that the Plantaginaceae are rather homogeneous chemically. Hegnauer discovered that species of both *Plantago* and *Littorella* produce aucubin (an iridoid glucoside; Jensen *et al.* indicated a common origin for all iridoid-containing taxa), and Bourdu *et al.* showed that species of these two genera store the same saccharides (stachyose being the most abundant) in comparable proportions in the roots and stems. The seeds of *L. uniflora* contain planteose and saccharose; those of *Plantago* have planteose but in some species stachyose as well (Bourdu *et al.*, Bourdu & Gorenflot). Wallaart identified sorbitol (a sugar alcohol) from the leaves of *L. uniflora* and ten species of *Plantago* and considered the accumulation of this hexitol to be a family character. Aucubin and planteose were also identified in the seeds of eight species of *Plantago* (including *P. major* L.) in Egypt (Ahmed *et al.*).

Chemical evidence has also suggested that the Plantaginaceae are much more closely related to the Scrophulariaceae than to either the Plumbaginaceae or the Primulaceae (Bourdu *et al.*, Gibbs, Hegnauer). Aucubin has been found as well in the Globulariaceae, Loganiaceae, Orobanchaceae, and Scrophulariaceae (Bate-Smith). The production of mannitol (a stereoisomer of sorbitol) by two species of *Plantago* also indicates a strong biochemical link with the Scrophulariaceae, according to Wallaart. The Plumbaginaceae and Primulaceae are among 68 families in which both leuco-anthocyanins and trihydroxy constituents have been identified, while the Scrophulariaceae and Plantaginaceae are among 70 families in which these compounds are not known (Bate-Smith). Seigler reported that while members of the Plumbaginaceae and Primulaceae do not have iridoid monoterpenes, such compounds have been found in about 41 other families, including the Scrophulariaceae and the Plantaginaceae. According to Alston and Turner, both the Scrophulariaceae and the Plantaginaceae are among about 20 families, exclusive of the Plumbaginaceae and the Primulaceae, in which linoleic acid and oleic acid are the major fatty acids.

The most common and widespread (and therefore, presumably, the ancestral) base chromosome number in the Plantaginaceae is six. (The Scrophulariaceae have six among their base numbers, but only the Plumbaginaceae have chromosomes with any morphological similarity to *Plantago* [McCullagh].) Diploids, triploids, tetraploids, hexaploids, octaploids, 12-ploids, and 16-ploids (i.e., $2n = 12$, 18, 24, 36, 48, 72, and 96) are known in *Plantago,* while only diploids and tetraploids (in the same series) have been reported for *Bougueria* (Rahn) and *Littorella,* respectively. The base numbers five (diploids, tetraploids, hexaploids, and decaploids) and four (diploids and tetraploids) have been reported in *Plantago* and are less common in the family. Aneuploids at numerous levels have also been reported in *Plantago* (see primarily Bolkhovskikh *et al.*).

Species of *Plantago* and *Littorella* shed binucleate pollen, except that that of *P. lanceolata* L. is trinucleate (Brewbaker). *Bougueria* is evidently unknown in this regard.

The pollen in the Plantaginaceae (which provides no clear indication of the systematic placement of the family [Erdtman]) is usually spheroidal (but sometimes ovoid or irregular) and more or less distinctly periporate, with the pores circular or irregular in shape. After some initial confusion that appears to have been resolved by the use of scanning electron microscopy, there is now agreement that the sculpturing is more or less verrucate. Although the outermost layer of ornamentation has been alternately described as micro-echinate (Bassett *et al.*, Bassett & Crompton) or scabrate (Clarke & Jones), the latter is the more appropriate term (according to Clarke & Jones) because the projections are rounded. Discrepancies regarding the presence or absence of annuli and opercula also exist in the literature, apparently because of a failure to recognize that within the family a continuum exists between grains possessing and those completely lacking such features (Clarke & Jones).

Because only four species of the Plantaginaceae are in genera other than *Plantago,* studies of topics such as embryology, anatomy, and morphology have mostly involved only species of *Plantago* and are therefore summarized in the generic discussion.

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YOUNG, D. J., & L. WATSON. The classification of dicotyledons: a study of the upper levels of the hierarchy. Austral. Jour. Bot. **18:** 387–433. 1970. [Data on 83 attributes of 543 genera; *Plantago* has characteristics of both "asclepioids" and "acanthoids" (but more in common overall with the latter, which includes the Scrophulariaceae and six other families).]

1. **Plantago** Linnaeus, Sp. Pl. **1:** 112. 1753; Gen. Pl. ed. 5. 52. 1754.

Erect or suberect, acaulescent (but sometimes branched near the base and/or rhizomatous) [or caulescent (and branched)], terrestrial, annual, biennial, or perennial herbs [or occasionally woody subshrubs]. Leaves simple, linear, lanceolate to oblanceolate, spatulate, ovate, or cordate; alternate, in basal rosettes [or, less frequently, alternate or opposite on sparsely to densely branched stems], exstipulate, with dilated, sometimes sheathing bases, glabrous or (rarely) densely pubescent (at least adaxially), entire, dentate, [or pinnatifid], one to many nerved, the blade and petiole distinct or not. Plants with only perfect flowers (or otherwise, usually with perfect and carpellate flowers on separate plants) [rarely dioecious]. Inflorescences axillary with cleistogamous or chasmogamous flowers sparsely to densely organized into long to short, cylindrical [to capitate] spikes. Flowers single in the axils of bracts, small, usually numerous, (chasmogamous flowers) mostly proterogynous and wind pollinated, and actinomorphic or slightly zygomorphic (with respect to corolla lobes). Sepals 4, imbricate, membranaceous-scarious, equal or in 2 unequal pairs (the abaxial pair sometimes connate in the basal half), alternate with the subtending bract, and often keeled [or rarely with many distinct nerves]. Corolla salverform with the tube ovoid to cylindrical and the 4 erect, spreading, or recurved lobes distinct, imbricate, membranaceous-scarious, and alternate with the sepals. Stamens 4 (occasionally 2), adnate to the corolla tube (rarely below the gynoecium), alternate with the petals; filaments filiform, induplicate in bud; anthers included or exserted, cordate, often apiculate, 2-locular, dorsifixed, versatile, and with longitudinal, latrorse to slightly introrse dehiscence. Carpels 2, connate; stigmas included or exserted; style filiform; ovary superior, 2-locular [or imperfectly

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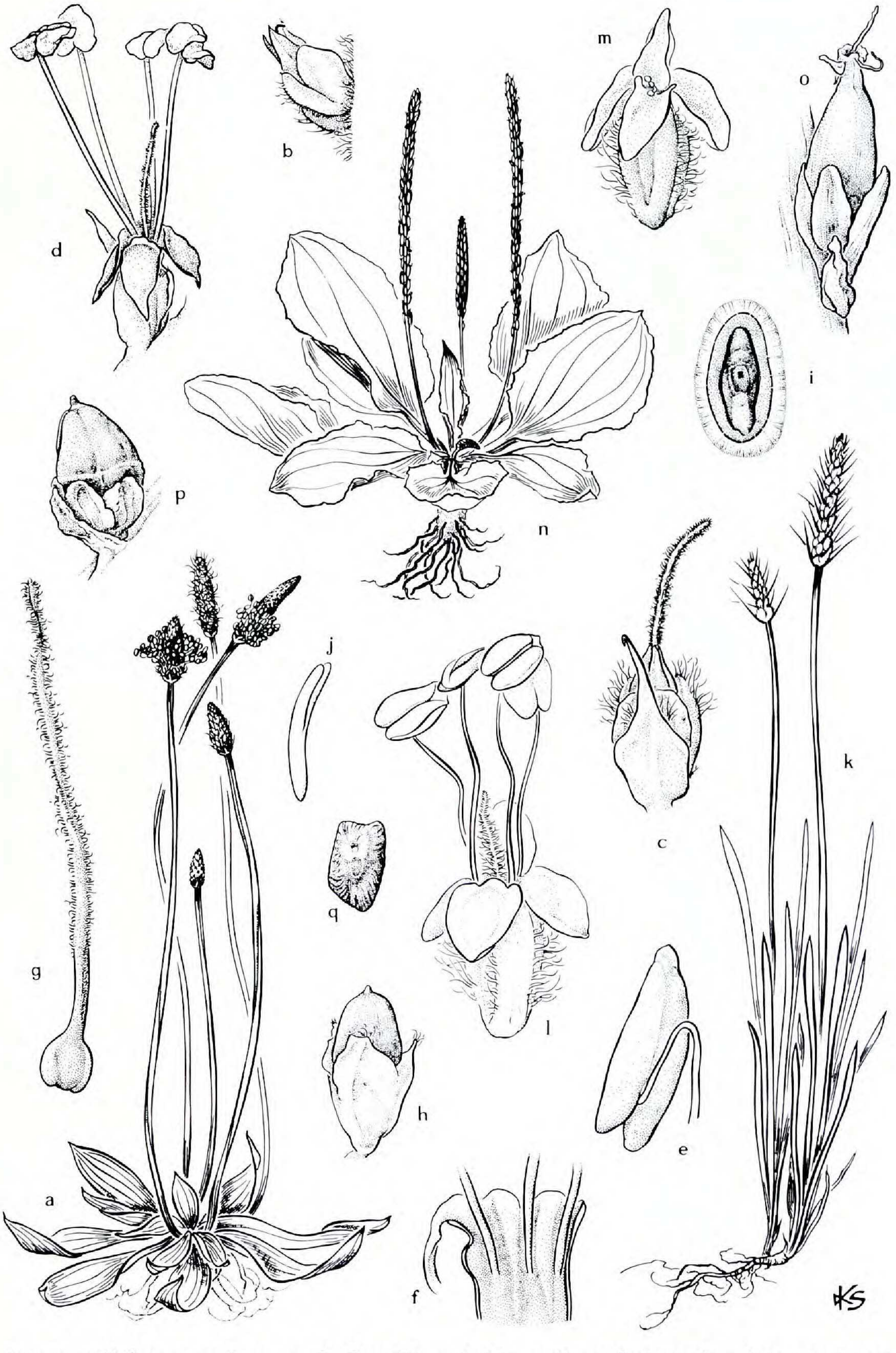
FIGURE 1. **Plantago.** a–j, *P. lanceolata*: a, habit, inflorescences with flowers immature, or with only styles protruding, or at anthesis, × ½; b, flower bud subtended by bract, × 6; c, flower with receptive style protruding, subtending bract in front, × 6; d, flower, later stage with corolla lobes open and anthers dehiscing, × 6; e, versatile anther, × 12; f, portion of corolla tube in section, filament bases inserted between folds of corolla, × 12; g, gynoecium, × 12; h, capsule surrounded by persistent calyx, × 6; i, adaxial surface of moistened seed, outer layer mucilaginous, × 6; j, embryo, × 6. k–m, *P. aristata*: k, habit—note long inflorescence bracts, × ½; l, flower at anthesis, × 6; m, "cleis-



togamous" flower, × 6. n, o, *P. Rugelii*: n, habit, × ½; o, fruit enclosed in persistent corolla tube, × 6. p, q, *P. major*: p, fruit with circumscissile line of dehiscence, × 6; q, adaxial surface of seed, × 12.

3- or 4-locular by the intrusion of false septa from the carpel midrib]. Ovules 1 to many per locule, tenuinucellar, hemianatropous to anatropous, integument single, massive; placentation axile. Fruit a globose to elongate capsule, circumscissile at or below the middle [indehiscent in *P. macrocarpa* Cham. & Schlecht.]; calyx persistent, the corolla usually so (but then irregularly torn about the middle of the tube). Seeds yellow-tan to almost black, often shining, for the most part narrowly elliptic in longitudinal median section (through the widest dimension of the seed); seed coat more or less mucilaginous when wet; endosperm cellular, fleshy; embryo parallel to the long axis of the seed and straight or sometimes curved. (Including *Coronopus* Miller, non Zinn, nom. cons., and *Psyllium* Miller.) LECTOTYPE SPECIES: *P. major* L.; see Britton & Brown, Illus. Fl. No. U.S. & Canada, ed. 2. **3:** 245. 1913. (*Plantago* listed by Linnaeus [Critica Botanica, p. 110. 1737; p. 87 in A. Hort, English transl., 1938] as a Latin name given by the "Ancients" [Pliny and other Roman writers]. According to Clute, and most others who have commented on the issue, the name is from Latin *planta,* signifying the sole of the foot, and *ago,* used in plant names in the sense of "wort" [but also to mean having the characteristics of].)—PLANTAIN.

A nearly cosmopolitan genus occurring largely in the Temperate Zones but only poorly represented in the lowland tropics, *Plantago* is recognized in the most recent worldwide monograph (Pilger) to consist of 258 species. Although perhaps best known for its nearly ubiquitous weedy members (*P. lanceolata* L. and *P. major* L., for example, are extremely widespread and even occur at low elevations in the New World tropics [D'Arcy; Dietrich, 1979]), most species are in fact of much more restricted distribution. Some are endemic to very small areas and/or are highly specialized ecologically. The genus is best represented in the Mediterranean region, the Himalayas, southwestern North America, and the mountains of South America.

Since Linnaeus (Species Plantarum, 1753) grouped the species of *Plantago* into those with *scapo nudo* and those with *caule ramosa,* suprasectional taxa have been recognized in the genus by Barnéoud (1844; two units based on seed number per capsule and seed shape in transverse median section), Harms (in Harms & Reiche; two subgenera based on leaf arrangement), Pilger (two subgenera based on leaf arrangement), and Rahn (1978a; three subgenera based on ovule/seed number per ovary/capsule, seed shape in transverse median section, corolla-tube pubescence, leaf shape, embryo orientation [plane between the cotyledons either parallel, oblique, or perpendicular to the adaxial surface of the seed], and chromosome number). The genus has also been divided into various numbers of sections by Barnéoud (1844), Decaisne, Harms (in Harms & Reiche), Pilger, and Rahn (1978a) based on different combinations of characters including spike morphology (size, shape, and flower arrangement and density), corolla pubescence, corolla-lobe shape, anther and stigma inclusion or exsertion, seed size, seed number per capsule, seed shape (in transverse median section as well as longitudinal median section through the widest dimension of the seed), leaf shape, degree of stem lignification, plant duration, and geographic distribution. Rahn (1978a) recently typified a number of subgeneric and sectional names in *Plantago,* and his infrageneric classification is followed here.

Approximately 24 indigenous and eight naturalized species of *Plantago* representing all three subgenera and ten of the sections enumerated by Rahn (1978a) occur in North America. Twelve (or perhaps 13) species in two subgenera and six (or perhaps seven) sections grow in the southeastern United States. The first four sections discussed below were placed in subg. PLANTAGO; the last three in subg. PSYLLIUM (Miller) Harms in Harms and Reiche. Ten of our species are indigenous to North America, and four of these appear to be naturalized in the Southeast (i.e., are native to other parts of the continent).

The predominantly Old World sect. PLANTAGO (fibrous-rooted perennials with petiolate leaves, elongate-cylindrical spikes, exserted anthers and stigmas, and 4–20 seeds per capsule) comprises about 19 species, including a closely related pair occurring in the Southeast. *Plantago major,* $2n = 12, 18, 24$, thought to be a native of Europe and northern and central Asia but now established throughout most of the rest of the world, is a weed that reportedly occurs in most parts of our range, although it is poorly collected and/or perhaps rare in our area. *Plantago Rugelii* Dcne., $2n = 24$, originally native to eastern North America, is a weedy species now widely established westward but at best uncommon outside of this continent. (It grows at or near sea level in Cuba [Dietrich, 1979] and has evidently become established in northern Europe [Hansen].) *Plantago Rugelii* occurs throughout the Southeast, but it seems to be poorly represented, if not absent, in peninsular Florida. *Plantago Rugelii* differs from *P. major* in its more elongate capsules that dehisce closer to the base and often contain fewer seeds; otherwise the species are remarkably similar morphologically. Although *P. major* and *P. Rugelii* usually grow (but not necessarily together) in fields, lawns, roadsides, sidewalks, and paths, both Tessene (1968) and Bassett (1973) have reported that *P. major* does not thrive in shaded and/or continually wet places and that *P. Rugelii* may be found in open woods and along damp shorelines. Hamilton and Buchholtz, however, counted significantly fewer seedlings of *P. Rugelii* in shaded plots than in open ones (all plots naturally seeded). *Plantago major* may be particularly well adapted to areas where the soil has been trampled (Blom; Sagar & Harper, 1960; Warwick) or compacted (Blom; see, however, Noe & Blom and Tessene, 1968). Hawthorn and Cavers (1976) found that in natural (pasture) populations, *P. Rugelii* had a longer half-life than *P. major* with regard to both seedlings and mature plants, while individuals of *P. major* flowered in greater numbers (proportionately) and earlier in development. Several authors have reported that *P. major* can be either an annual or a perennial (see Hawthorn & Cavers, 1976).

Four of the six species comprising the Old and New World sect. MICROPSYLLIUM Dcne. (taprooted annuals with linear leaves and loose, elongate spikes bearing small flowers with usually two stamens and included anthers and stigmas) occur in North America (see Bassett, 1966), and the two present in our range, *Plantago heterophylla* Nutt., $2n = 12, 22$, and *P. pusilla* Nutt., $2n = 12$, are nearly indistinguishable. Both have erect corolla lobes, but *P. heterophylla* has many (usually 10–25) small seeds per capsule, while the fruits of *P. pusilla* almost invariably contain four larger seeds.[2] Very small individuals occur in both species. *Plantago heterophylla* is more common than *P. pusilla* in the Southeast (in North America it is almost restricted to our area). It grows in moist, sandy or silty soils and is frequently a weed in cultivated or waste places. It is an adventive in California (Pilger) and in the northeastern United States (northward to southern New York [Bassett, 1966]), but it is evidently indigenous in Argentina and Paraguay (Pilger). *Plantago pusilla* is most often found in disturbed areas. Its rather limited natural range includes the southern three-fourths of Missouri and adjacent states. *Plantago pusilla* has become established in the East from North Carolina to Massachusetts, and more sporadically in the West between southern California and southwestern Washington (Bassett, 1966). In our area, therefore, it occurs as a native in Arkansas and Tennessee and as an adventive in northeastern North Carolina.

The nearly cosmopolitan and rather poorly distinguished sect. PALAEOPSYLLIUM Pilger (thick-rooted perennials with ovate-cordate to oblanceolate leaves having relatively distinct petioles; loose, elongate spikes bearing large flowers with exserted anthers and stigmas; and two to nine seeds per capsule) consists of about 28 species, of which four are North American (see Bassett, 1967). Two of these occur in the Southeast.

Plantago cordata Lam., $2n = 24$, has distinctly petiolate leaves with ovate to cordate blades and veins that appear to arise from a midrib (vs. from the base of the blade, as in the rest of the genus), hollow scapes, sepals that are about as long as the bracts, and two- to four-seeded capsules that dehisce approximately at the middle. The species is unique in the genus in that the fruits are still green and alive at the time of dehiscence, when the lid of the pyxis readily falls off, and the two or three seeds with the entire fleshy placenta fall out as a unit (Tessene, 1969). This structure is buoyant and may represent an adaptation to dispersal by water. The plants grow in alluvial woods, on wet rocky banks, in streams through areas of slate bedrock, and in the shallow soil of cedar (*Juniperus virginiana*) barrens in our area. The species probably occurs in all of the southeastern states, although it is perhaps absent from southern Florida and is apparently unknown outside of North America. *Plantago cordata* differs from *P. major* and *P. Rugelii,* with which it is often confused, in a number of ways. Its leaves are larger, the blades are more abruptly contracted to the petiole (but not always cordate), and the major veins, although actually parallel, approach a pinnate arrangement. In addition, the roots are thicker and the flowering time is earlier in *P. cordata*.

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[2] *Plantago heterophylla* Nutt. (1835; see Foster) has been the most commonly used name for the plants with ten or more seeds per capsule. Godfrey and Wooten used the earlier name *P. hybrida* W. Barton (1818) for this species and incorrectly listed *P. elongata* Nutt. (instead of *P. heterophylla*) in synonymy. The species with four seeds per capsule has been called *P. elongata* Pursh (1814) or *P. pusilla* Nutt. (1818), depending on taxonomic interpretation, the later name being used if our eastern plants are considered to be specifically distinct from more western populations. Unfortunately, seed number is mentioned in none of the four protologues involved, and I have not been able to study the type specimens. To minimize the likelihood of adding confusion, I have chosen to use the most commonly employed names, *P. heterophylla* and *P. pusilla,* although the reader should be aware that the situation is subject to change.

The second species, *Plantago sparsiflora* Michaux, $2n = 24$, has oblanceolate leaf blades that gradually taper to the petiole, scapes that are only sometimes hollow, sepals that are about twice as long as the bracts, and two-seeded capsules that dehisce below the middle. It is known only from the Coastal Plain of northern Florida and the southeastern portions of Georgia and the Carolinas, where it is frequent in wet or dry savannas, roadsides, and ditches.

Tessene (1969) studied in detail many aspects of *Plantago cordata,* which he considered to be the rarest North American species of the genus. He determined that the characteristic venation of the leaf, so frequently used to distinguish the species, usually does not develop until after fruiting has begun, and that depauperate inflorescences often retain solid peduncles. He stated that it usually grows in calcareous substrates and reported only one instance in which the species was found in a disturbed, man-made habitat (an unshaded drainage ditch). Tessene also attempted crosses between *P. cordata* and eight other species in four sections of *Plantago,* with only one F_1 plant resulting. This hybrid, *P. cordata* × *P. eriopoda* Torrey (both of sect. PALAEOPSYLLIUM) was sterile and intermediate in most characters.

The New World sect. VIRGINICA Barn. (leaves elliptic to spatulate, often dentate; scapes long and with a terminal, many-flowered, cylindrical spike; abaxial sepals much narrower than the adaxial ones; corolla tubes glabrous and lobes erect or spreading; capsules with up to four but usually two or three seeds) was the subject of an ambitious revision based primarily on the morphology of herbarium specimens but influenced by ecological data, cultivation experiments, chromosome studies, hybridizations, and taximetric analyses (Rahn, 1974). Included were sections OREOPHYTUM Dcne., CLEIOSANTHA Dcne., and NOVORBIS Dcne., in addition to species from sections PALAEOPSYLLIUM and LEUCOPSYLLIUM Dcne. Twenty-eight species (four described as new) were recognized in the section (morphologically indistinguishable entities differing in chromosome number were treated as conspecific); five of these occur in North America, and two are found in the Southeast. Both have concave adaxial seed surfaces (vs. plane in the three other species) and are annuals with slender primary roots, pilose leaves, spreading hairs on the scape, erect corolla lobes, and two-seeded capsules.

Plantago virginica L., $2n = 12, 24$ (or ca. 24 [Rahn, 1974]), occurs throughout the eastern half of the United States, including all of the Southeast, and is apparently a waif in southern Ontario (Bassett, 1973). It is more sporadically distributed in the western states and northeastern Mexico. The species appears to be a spring ephemeral (Rahn, 1974; all but four of the 111 specimens I examined were collected earlier than June) and is generally found in dry, sandy soils of waste places, fallow and cultivated fields, and roadsides. *Plantago virginica* can be distinguished from the other common plantagos in our area by its dentate, spatulate leaves, its rather dense, cylindrical spikes, and its persistent corollas with conspicuous, yellow, erect lobes. Depauperate forms of the species are fairly common.

Plantago rhodosperma Dcne., $2n = 24$, occurs in rocky or sandy soils mainly in the southwestern United States and adjacent Mexico. Although Rahn (1974) cited no specimens from our range (and I have seen none), his distribution map for the species includes Louisiana, most of Arkansas and Mississippi, and southwestern Tennessee. Several other authors (Correll; Small, 1913; Smith; Steyermark) have reported the species from various combinations of these states. *Plantago rhodosperma* differs from *P. virginica* in having acuminate to mucronate (vs. obtuse) abaxial sepals, and broad (vs. narrow) seeds with shallowly (vs. deeply) concave adaxial sides.

The Old World sect. LANCIFOLIA Barn. (sect. *Arnoglossum* Dcne.) (oblanceolate leaves, grooved peduncles, dense spikes, and abaxial sepals fused for more than half their length) consists of perhaps six species, one of which is represented in our area. *Plantago lanceolata,* $2n = 12$, 13, 24, 96, native to Europe and northern and central Asia, is established throughout most of the world, especially in temperate regions. It is an extremely variable species that is widely distributed across temperate North America (except the prairie provinces of Canada) and Mexico in most kinds of disturbed habitats. Perhaps the best-known member of the genus, *P. lanceolata* has been an extremely popular subject for research, some of which is summarized below. (See also Cavers *et al.* for a synthesis of much of the recent information concerning many aspects of its biology.)

Plantago sect. GNAPHALOIDES Barn. (flowers paired or in threes; hairs of the scape wider than those of the leaves, and at least some hairs ascending) comprises the American species included by Pilger in sect. LEUCOPSYLLIUM and was divided into four series by Rahn (1978a). The seven North American species, all $2n = 20$, are in series *Gnaphaloides* Rahn (annuals with well-developed taproots; linear leaves [but wider than those of species in sect. MICROPSYLLIUM]; spikes dense, cylindrical; bracts, especially of the lowermost flowers, often with an elongated green nerve; corolla lobes relatively conspicuous and recurved, with cordate to obtuse bases; and anthers small). Five species, including the three that occur in our range, have zygomorphic corollas with cordate lobes (vs. actinomorphic with slightly cordate or obtuse lobes in the two other species). Of our species, *P. aristata* Michaux and *P. Wrightiana* Dcne. (*P. Hookeriana* Fischer & Meyer var. *nuda* (Gray) Poe) are more common and have adaxial leaf surfaces that are glabrous or nearly so; in the less common *P. patagonica* Jacq. (*P. Purshii* Roemer & Schultes) these surfaces are densely hairy.

Plantago aristata is easily recognized by its conspicuous, often leaflike bracts that are usually smaller toward the apex of the spike. Taxonomically insignificant depauperate individuals with very narrow leaves, reduced flowers, and hairy, few-flowered spikes can be found, but such inflorescences occur on otherwise normal plants, and all intermediate forms exist. *Plantago aristata* is a common weed throughout the eastern United States (with the exception of the extreme north). It grows most commonly in dry, sandy soil along roadsides and in pastures, fields, and other kinds of recently disturbed habitats. It is an adventive in Oregon and California and in various parts of the Old World (Rahn, 1978b). *Plantago Wrightiana* differs most obviously from *P. aristata* in having shorter (and therefore less conspicuous) bracts. According to Rahn (1978b), the species occurs in three disjunct areas: central Arizona; Oklahoma, Texas, and adjacent parts of Mexico; and parts of Mississippi, Alabama, Georgia, Florida, and the Carolinas. (I have, however, seen herbarium specimens from Louisiana and southwestern Arkansas that cast doubt on Rahn's contention that the southeastern populations are disjunct from those in Texas and Oklahoma.) Rahn also stated that, on the basis of ecological data, *P. Wrightiana* is probably not native to our area.

The third of our species in series *Gnaphaloides, Plantago patagonica,* is intermediate in bract width and length between *P. aristata* and *P. Wrightiana.* It is at least an adventive in the Southeast. I have seen three specimens of *P. patagonica* (two were annotated by Rahn in 1975): one from railroad tracks in Cleveland Co., Arkansas, and two specimens from a roadside in Lancaster Co., North Carolina. (Smith has also reported it from Arkansas.) The species is otherwise known from southern and central Argentina; from an area between northern Baja California and south-central British Columbia eastward to the western Great Lakes and central Texas; and from two localities in interior New England (Rahn, 1978b).

Species of sect. PSYLLIUM (Miller) Lam. & DC. (branched, caulescent herbs or subshrubs with opposite or rarely whorled leaves) are native to the Mediterranean region and the Middle East. *Plantago Psyllium* L.,[3] $2n = 12$, an annual with dense, subcapitate spikes and a taproot, has been reported from various parts of the world. In North America it has been collected in sandy and/or waste places. *Plantago Psyllium* is rare in southern Canada (Bassett, 1973), occasional in the northwestern United States (Hitchcock & Cronquist), known from many parts of California because it is often a constituent of commercial bird-seed (Munz), and well established in the eastern United States (Gleason & Cronquist). It is rare and perhaps not persistent in our area. Although it has been reported from coastal dunes in North Carolina (New Hanover Co.; Radford *et al.*), I have seen neither a voucher specimen for this station nor any other specimen from the Southeast.

Cytological studies have provided data that bear, either alone or in combination with palynological information, on various systematic problems in the genus. McCullagh, who studied mitosis in the root tips of 40 species of *Plantago* (including *P. major, P. lanceolata, P. patagonica,* and *P. Psyllium* and allied species), recognized six morphological types of chromosomes. McCullagh concluded that the genus is monophyletic (with new species having arisen by polyploidy, reduction in the number of chromosomes, and hybridization—the latter two processes often followed by chromosomal duplication), and that differences in chromosome morphology do not correlate with the two subgenera based on leaf arrangement (cf. Harms in Harms & Reiche; Pilger). The Old World and American species included by Pilger in sect. LEUCOPSYLLIUM were considered by Rahn (1978a) to form morphologically distinct groups and were therefore placed by him in sections ALBICANS Barn. and GNAPHALOIDES, respectively. This position was reinforced by Bassett and Crompton, who observed that *P. fastigiata* E. L. Morris (*P. insularis* Eastw.) differs from the other North American species of sect. LEUCOPSYLLIUM (i.e., those included in sect. GNAPHALOIDES by Rahn) in several ways, including chromosome number ($2n = 8$ vs. 20) and pollen morphology (for example, smaller grains with operculate pores). Thus, although sections ALBICANS and GNAPHALOIDES appear to be taxonomically distinct, the former is not confined to the Old World and is therefore not geographically isolated from the latter, as was implied by Rahn (1978b). Finally, although both Wodehouse and Bassett (1973) have remarked that *P. major* and *P. Rugelii* differ more palynologically than morphologically, such differences could be due to chromosome number alone: the grains of *P. Rugelii,* a tetraploid, are larger and have more numerous pores than those of *P. major,* primarily a diploid.

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[3] There has been some confusion about the nomenclature of this species. Linnaeus (Species Plantarum, 1753, p. 115) described *P. Psyllium* with the phrase "caule ramoso, foliis integerrimis, spicis foliosis," but later (Systema Naturae, 1759, p. 896) used the description "caule ramoso suffruticoso, foliis integerrimis, spicis aphyllis" for *P. Psyllium* and "caule ramoso herbaceo, fol. integerrimis, spicis foliosis" for a new species, *P. indica.* Panigrahi has treated *P. indica* L. (1759) as an illegitimate synonym of *P. Psyllium* L. (1753), and that name in turn as a nomen confusum. The name *P. arenaria* Waldst. & Kit. has been used by Shear and by Chater and Cartier (in Moore, 1976), who listed (in synonymy) *P. Psyllium* as a nomen ambiguum and *P. indica* as a nomen illegitimum.

An interesting anatomical feature of *Plantago* is the occurrence of cambiform tissue in the cortex and/or pith of the fleshy rhizomes of many species, particularly those in sect. PLANTAGO (Metcalfe & Chalk). These rows of cells appear to represent incompletely developed vascular bundles and are apparently connected with one another (but not with the bundles of the vascular ring). In *P. major* and *P. media* L. they become converted into true medullary vascular bundles.

The tendency for insular members of a group to be more woody than their continental relatives is exemplified by species of *Plantago* (Carlquist). The ability to accumulate secondary xylem has evolved independently in this genus several times, apparently in response to the relative uniformity of island climates. The adaptation of these same species to wetter conditions following migration from drier continental areas has involved an increase in vessel element length and diameter. In *Plantago,* as in other groups of predominantly herbaceous dicots, wood produced by insular species is largely rayless.

Nodal anatomy in *Plantago* is extremely variable and a poor indicator of infrageneric relationships (Misra, 1966). Species in such dissimilar groups as sections CORONOPUS (Miller) Lam. & DC. (of subg. CORONOPUS (Miller) Rahn) and PSYLLIUM (of subg. PSYLLIUM) are unilacunar, while *P. ovata* Forskål (sect. ALBICANS of subg. PSYLLIUM) is trilacunar and *P. Lagopus* L. (sect. LANCIFOLIA of subg. PSYLLIUM) and *P. major* (sect. PLANTAGO) are multilacunar. Anatomical complexity at the nodes appears to be a function of leaf size because unilacunar nodes are found in species with narrow leaves and bases and multilacunar types are associated with broad leaves and sheathing bases.

The presence of an endodermis with Casparian thickenings has been noted in both stems (Metcalfe & Chalk) and leaves (Trapp) in species of *Plantago.* Trapp found that in each of eight examined species (including *P. lanceolata* and *P. major*), the leaf endodermis is structurally no different than that found in angiosperm roots, and experiments showed that it is even potentially capable of arresting the outward diffusion of solutes. He considered it improbable, however, that such a function is actually realized and concluded that the presence of a foliar endodermis in these plants appears to be neither beneficial nor detrimental to a leaf's functioning.

Leaves of *Plantago* often resemble those of monocotyledons in their narrowness, parallel venation, and sheathing bases. Even species with distinct petioles and blades are often said to be pseudo-laminate, the blade representing (as in monocots) an "expansion of the apical region of the original phyllode" (Arber, 1918). Furthermore, leaf development involves the cessation of intercalary activity and the subsequent maturation of tissues in a basipetal direction, as is well expressed in monocots but is also seen in conifers and other dicots with narrow leaves (Esau).

The stomata of young leaves of *Plantago* are anomocytic (ranunculaceous); those of adult leaves are various (Moncontié). Stomata are usually diacytic (caryophyllaceous) in a number of species, including *P. lanceolata* and *P. Psyllium,* but they are rarely so in *P. major.* They may be distributed either on both surfaces of the leaf (e.g., as in *P. lanceolata, P. major,* and *P. Psyllium*) or (as in two extraregional species) only abaxially (Metcalfe & Chalk). In *P. lanceolata* and the extraregional *P. altissima* L. stomatal size appears to be positively correlated with chromosome number (Moncontié).

The floral anatomy of *Plantago lanceolata, P. major,* and *P. Rugelii* has been studied by Henderson, whose observations suggested that the bract in *Plantago* actually represents a fifth sepal. Henderson observed, among numerous other things, that the stamens separate from the receptacle as a ring of tissue (remaining connate for some distance up the ovary) and are never fused to the corolla in *P. lanceolata* and *P. major*; my own observations, however, reveal that they are indeed epipetalous, as she correctly indicated for *P. Rugelii.*

The ovule in *Plantago* has a single, massive integument and is tenuinucellar (the archesporial cell develops directly into the megaspore mother cell). It has been described as anatropous by Cooper (for *P. lanceolata,* although his illustration showed it to be more similar to what is usually considered hemianatropous), anacampylotropous by Misra (1964, for *Plantago*), hemianatropous to anatropous by Davis (for the family), anatropous to hemitropous by Cronquist (1981, for the family), and more or less anatropous, erect, or anacampylotropous by Corner (for the family). Ovule and seed development in *P. lanceolata* have been described in great detail by Cooper (see also Davis; Misra, 1964), who stated that the megagametophyte in this species is of the Polygonum type. Although Cooper also indicated that the basal cell of the zygote forms the suspensor, Davis stated that the embryogeny is of the Onagrad type. The presence of both micropylar and chalazal haustoria in the developing seed was noted above (family discussion).

Circumscissile dehiscence of the fruit occurs in such disparate genera as *Plantago* and *Celosia* (Amaranthaceae), *Anagallis* and *Centunculus* (= *Anagallis*) (Primulaceae), *Portulaca* and *Lewisia* (Portulacaceae), and *Hyoscyamus* (Solanaceae). In each of the species of *Plantago* studied by Rethke (including *P. major* and *P. pusilla*), the cells near the region of future dehiscence remain meristematic through much of fruit maturation. These cells are smaller and have thinner walls than adjacent epidermal and/or subepidermal cells. Dehiscence results from the breaking and separation of cells in this zone of mechanical weakness and occurs as the drying capsule shrinks against the mature, unyielding seeds (see also Lamba & Gupta).

The extent to which genotype (vs. environmental factors) determines phenotype, including morphological oddities, has received considerable attention. Evidence has suggested that while branched spikes are under genetic control in *P. lanceolata* (Weatherwax; cf., however, Yamaura) and *P. major* (Hammarlund), they seem to result from external factors in *P. Rugelii* (Weatherwax). The lengths of scapes, capsules, seeds, and bracts (as well as the number of flowers produced) were all found to be positively correlated with plant size in *P. aristata* (Goodwin), which is evidently not genetically determined. It is notable that depauperate plants sometimes produce lowermost bracts that do not exceed the flowers they subtend, and that they may thus rather closely resemble several other species of sect. GNAPHALOIDES. In a series of long-range experiments involving both cuttings and seedlings, Marsden-Jones and Turrill found that plant size and peduncle pubescence in *Plantago major* were mostly determined by the soil in which the plants were grown (cf., however, Warwick & Briggs, 1979).

A number of studies have been undertaken to determine the relationship between phenotype and ploidy level in *Plantago.* Chandler (1954) showed that pollen size, seed size, quantity of mucilage, and plant vigor are all greater in colchicine-induced tetraploids (compared to the corresponding diploids) in *P. rhodosperma, P. Wrightiana,* and the extraregional *P. ovata.* In *P. ovata* such treatment resulted in larger leaves with generally larger cells, larger stomata, and broader epidermal hairs (Chandler & Barton). Several physiological differences were also noted, including the fact that tetraploids are, in general, developmentally slower than diploids. It is also interesting that the amount of aucubin (see family discussion) did not differ between the two groups. In other studies involving extraregional species, Rahn (1954) discovered that in *P. media* the seed number per capsule, scape length, and leaf size are all greater in natural tetraploids than in diploids (although pollen diameter and stomatal size do not differ), and Böcher *et al.* found in *P. Coronopus* L. that the anthers, flowers, and plants themselves are larger in natural hexaploids than in diploids.

Hybrids involving species of *Plantago* represented in the Southeast have apparently not been encountered (with the exception of the artificially produced *P. cordata* × *P. eriopoda* [Tessene, 1969]). Artificial crosses between *P. major* (sect. PLANTAGO) and *P. lanceolata* (sect. LANCIFOLIA) were unsuccessful (Rahn, 1957). In fact, hybrids involving these two species, either together or with other species, are not known (Sagar & Harper, 1964). No hybrid in which *P. major* was a parent has been reported, and the identity of herbarium specimens of a putative hybrid between *P. lanceolata* and the extraregional *P. media* (sect. LAMPROSANTHA Dcne. of subg. PLANTAGO) is doubtful. All attempts to produce artificial hybrids between *P. media* and either *P. major* or *P. lanceolata* have failed. Attempted crosses between extraregional species in sect. LAMPROSANTHA and those in sects. PLANTAGO, LANCIFOLIA, and CORONOPUS have also been unsuccessful (Rahn, 1957). Also among species not occurring in the Southeast, natural introgressive hybridization was reported in subg. CORONOPUS sect.

MARITIMA H. Dietr. (Cartier, 1971, 1972), and a high degree of interfertility was observed in subg. PSYLLIUM sect. MONTANA Barn. when artificial crosses involved plants with the same chromosome number (Cartier, 1973).

The occurrence of perfect and carpellate flowers on separate plants (gynodioecy) has been observed, investigated, and discussed since the time of Darwin. *Plantago lanceolata,* in particular, has been the subject of a number of investigations (see Bartlett, Ludwig, and Ross [1969]). Ross proposed that there are dominant alleles at two loci for perfect flowers, so double homozygous recessive individuals produce only carpellate flowers (cf., however, Atal, Van Damme & Van Delden, and Krohne *et al.* regarding a possible cytoplasmic effect). Because such individuals contribute genes to subsequent generations through ovules only, it is reasonable to postulate the existence of a compensatory mechanism by which carpellate-flowered plants are maintained in populations in which plants with perfect flowers contribute genes through both ovules and pollen and are therefore presumably at a selective advantage. Krohne *et al.* determined, in fact, that in natural populations (in northern California) carpellate plants generally produce more seeds than do those with perfect flowers (see also Primack, 1978).

Plantago lanceolata is also self-incompatible, even though such a system might appear to reinforce the process of outcrossing unnecessarily. Investigations by Ross (1973) suggested that at least four alleles at a single locus are involved, and that incompatibility results if the pollen has either of the alleles present in the style. (Unlike most other angiosperms with trinucleate pollen, the incompatibility is gametophytic.) Ross (1973) argued that matings between wholly perfect or wholly carpellate progeny (which could result from individual maternal parent plants with perfect or carpellate flowers, respectively) would be limited by self-incompatibility in the first case (there would be no limitation on such crosses under gynodioecy alone) and prevented by gynodioecy in the second (a portion of such crosses would be possible under the incompatibility system alone). In this way the two systems would be mutually reinforcing.

Plantago is usually considered to be primarily wind pollinated, at least in those species with chasmogamous flowers, and a majority of the evidence seems to bear this out. Many of the traits usually associated with anemophily (flowers proterogynous, small, unattractive, scentless; stigmas large, pubescent; anthers large, versatile on long filaments; and pollen spheroidal, dry, relatively smooth, with little variation in size) are found in species of *Plantago.* For example, on the basis of data gathered by Bassett and Crompton from North American plants, Primack (1978) demonstrated that variation in mean pollen diameter was greater among species with cleistogamous flowers than among those with chasmogamous ones. This presumably reflects selection against pollen that is either too large or too small (see also Proctor & Yeo).

Some species of *Plantago* appear to be at least partly entomophilous (but, as Proctor & Yeo have pointed out, bees sometimes collect pollen from plants that are anemophilous). Clifford stated that in Britain *P. lanceolata* is considered to be wind pollinated, but plants of it are regularly worked by honey bees for pollen whenever conditions are warm enough and a sufficient number of spikes are flowering within a few feet of one another. A more elaborate study of insect pollination in this species in the Netherlands (Stelleman & Meeuse) attempted to prove that pollen is actually transferred to the stigmas by flies of the genera *Melanostoma* and *Platycheirus* (Diptera: Syrphidae). Spikes of a group of donor plants were dusted with stained pollen of *P. lanceolata.* This pollen was later detected on both the flies and the stigmas of receptor plants located in a separate group upwind, while only negligible amounts of it were found on the donor plants' side of test slides placed between the two groups of plants.

Several investigations of reproductive biology have involved species of *Plantago* in the Southeast. Primack (1979) estimated that "reproductive output" is greater among annuals (vs. perennials), spring (vs. summer) annuals, and weedy (vs. nonweedy) perennials. Primack and Antonovics (1982) later found that in "reproductive effort" eight populations of *P. lanceolata* from the central Piedmont of North Carolina had a range of values comparable to that obtained by Primack (1979) for various perennial and/or weedy species of *Plantago,* but less than that determined for annual species (although the degree of genetic control was not clearly established). Primack (1980) also determined that phenotypic variation in *Plantago,* as measured by several criteria (number of inflorescences, number of capsules per inflorescence, number of seeds per capsule, and weight per seed), is no less in rare species than in more widespread ones. Significant differences in all of these measures except seed number per capsule were later observed under controlled conditions in *P. lanceolata* (Primack & Antonovics, 1981).

Studies involving *Plantago lanceolata* have shown that these plants may become physiologically adapted to very local conditions. Among populations in the Southeast, Wu and Antonovics (1976) demonstrated a greater tolerance to lead by roadside (vs. nonroadside) individuals, and Pollard showed essentially the same kind of response to zinc, copper, arsenic, and lead at sites contaminated with these metals. In contrast to various authors who have suggested that the wide geographic ranges characteristic of many weedy species are primarily the result of broad temperature optima for photosynthesis, Teramura and Strain demonstrated that substantial differences exist in the photosynthetic response to temperature among populations growing in relatively close proximity (eight meters to ten kilometers apart). Plants cloned from leaves taken from a shaded population were more sensitive to temperature extremes than were those propagated from open and sun-flecked populations that were exposed to much greater diurnal and seasonal fluctuations in temperature. Plants from the open population had much greater light-saturated rates of photosynthesis as well.

Plantago pollen has been helpful in studies regarding the effects of human activity on vegetation. Godwin (1975) pointed out that the increase in the number of records of *P. major* and *P. lanceolata* in British postglacial sediments corresponds to the progress of deforestation and the spread of agriculture by Neolithic man. (There are no corresponding increases involving such less weedy species as *P. media* and *P. maritima* L.) In the Vosges region of France, the degree of aforestation and cultivation is reflected in the relative abundance of the pollen of *P. lanceolata* in surface samples (Janssen).

The rather substantial, but frequently underestimated, economic significance of *Plantago* has been thoroughly discussed by Hammond. Several species, but especially *P. lanceolata* and *P. major,* are well known and noxious lawn weeds that also compete with crop plants for light, space, and nutrients (see Hammond; Higbee & Lee). Inadvertent dissemination of these plants results from *Plantago* seeds being unavoidably harvested with (and difficult to separate from) crop seeds. The leaves of *Plantago* do not dry readily and can therefore contribute to spoilage in hay that is sufficiently contaminated (Gill & Vear). *Plantago* species also act as hosts to a variety of viruses and (other) organisms known to cause disease in crops including beets, potatoes, turnips, cucumbers, tomatoes, broad beans, and tobacco. Precisely how this translates into economic loss is largely a matter of speculation at present.

Plantago lanceolata is sometimes fed to livestock as a mineral supplement, and it is still grown in the Netherlands for use in herbal remedies. *Plantago major* has also been used in this way for a variety of medicinal problems. The mucilaginous seeds of *P. Psyllium* and related species ("psyllium" seeds) act as a mild laxative and are harvested from crops raised specifically for this purpose. Chandler (1954) reported that almost four million pounds of psyllium seeds were imported into this country in 1953 and discussed the possibilities of domestic production for use of the mucilage in pharmaceutical preparations and as basic stabilizers in making ice cream, in printing and finishing, and in setting lotions (see also Morton). According to the United States Department of Agriculture, Foreign Agricultural Service, over 12 million pounds of psyllium seeds were imported into this country in 1981, at a value of over nine million 1981 dollars.

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the glucosinolate-myrosinase system. Pp. 43–79 *in* D. A. YOUNG & D. S. SEIGLER, eds., Phytochemistry and angiosperm phylogeny. New York. 1981. [Myrosin cells (protein-rich idioblasts in which myrosinase is thought to be concentrated) reportedly absent from the Plantaginaceae, even though hydrolysis products of glucosinolates have been reported from leaves of certain *Plantago* species (including *P. major*).]

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SMALL, J. K. Flora of the southeastern United States. ed. 2. xii + 1394 pp. New York. 1913. [Ten spp. of *Plantago* from our range.]

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SMITH, E. B. An atlas and annotated list of the vascular plants of Arkansas. iv + 952 pp. Published by author, University of Arkansas, Fayetteville, Arkansas. 1978. [*Plantago,* 251; nine spp. mapped, 252.]

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